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Salinity reduces radiation absorption and use efficiency in soybean

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Abstract

The potential rate of plant development and biomass accumulation under conditions free of environmental stress depends on the amount of radiation absorption and the efficiency of utilizing the absorbed solar energy to drive photosynthetic processes that produce biomass materials. Salinity, as a form of soil and water stress, generally has a detrimental effect on plant growth, and crops such as soybean are usually sensitive to salinity. Field and greenhouse experiments were conducted to determine soybean growth characteristics and the relative impact of salinity on radiation absorption and radiation-use efficiency (RUE) at a whole plant level. Cumulative absorption of photosynthetically active radiation ($\sum$APAR) was estimated using hourly inputs of predicted canopy extinction coefficients and measured leaf area indices (LAI) and global solar radiation. On 110 days after planting, soybean plants grown under non-saline conditions in the field accumulated 583 MJ $\sum$APAR m^{-2}. A 20% reduction in $\sum$APAR resulted from growing the plants in soil with a solution electrical conductivity (EC) of about 10 dS m^{-1}. Soybeans grown under non-saline conditions in the field achieved a RUE of 1.89 g MJ^{-1} $\sum$APAR for above-ground biomass dry materials. The RUE reached only 1.08 g MJ^{-1} $\sum$APAR in the saline soil, about a 40% reduction from the non-saline control. Salinity also significantly reduced $\sum$APAR and RUE for soybeans in the greenhouse. The observed smaller plant and leaf sizes and darker green leaves under salinity stress were attributed to reductions in LAI and increases in unit leaf chlorophyll, respectively. Reductions in LAI exceeded small gains in leaf chlorophyll, which resulted in less total canopy chlorophyll per unit ground area. Analyzing salinity effect on plant growth and biomass production using the relative importance of $\sum$APAR and RUE is potentially useful because APAR and total canopy chlorophyll can be estimated with remote sensing techniques.

Keywords: Salinity; Soybean; Radiation-use efficiency; Photosynthetically active radiation

1. Introduction

One of the most intriguing methods of forecasting the potential growth rate and yield of agricultural crops is to correlate plant growth and biomass production with the amount of absorbed solar radiation (Monteith, 1977). The approach is fundamentally sound because photosynthesis is the principal pathway of plant carbohydrate assimilation, and radiation is the only source of expendable energy essential for photosynthesis. For a crop species under non-stressed conditions, the rate of biomass accumulation can be expressed as the product of (1) the fraction of total photosynthetically active radiation (PAR) absorbed by

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the canopy and (2) the efficiency of utilizing the absorbed PAR to drive photosynthesis for biomass assimilation (Monteith, 1994). The amount of radiation that may be absorbed by a plant canopy is strongly related to the vegetation cover or LAI, canopy structure, and solar zenith angle. The efficiency of utilizing the absorbed PAR for biomass production, hereafter termed radiation-use efficiency (RUE), can change with variations in leaf chlorophyll content (Muchow and Davis, 1988), plant growth stage (Rochette et al., 1995), and field management practices and environmental stress levels. RUE increased with increasing nitrogen fertilization in wheat (Green, 1987). Depending on the timing of stress, drought reduced either the amount of absorbed radiation or RUE in barley (Jamieson et al., 1995). RUE also varied with row spacing in soybean (Board et al., 1994).

High levels of salinity can significantly reduce plant development such as shoot and root growth for many plant species, including soybean (Shannon, 1994). Growing soybeans in saline environments often leads to excessive uptake and accumulation of salt ions such as Na^+ and Cl^- in plant tissues (Läuchli and Wieneke, 1979). One explanation for the high tissue salt content is that salt flux to the shoot exceeds the rate of absolute shoot growth as shown in tomatoes (Dalton et al., 1997). Concentrations of the salt ions can reach toxic levels that would cause leaf injury and impair basic functions of photosynthesis and regulation of biochemical reactions and nutrient translocation (Greenway and Munns, 1980). The osmotic effect of salinity stress is to reduce substrate water potential, similar to water stress, but induced by the high solute contents. As indicated in Sionit and Kramer (1977), low levels of water stress can reduce soybean cell expansion and cell wall synthesis, and high levels of water stress would significantly increase stomatal resistance and reduce CO_2 assimilation. The combined osmotic and ion toxicity effect from salt stress often reduces canopy development in most plant species, and one would expect a reduction in season total absorption of PAR or $\sum$APAR. Salinity can also result in darker leaves such as in soybeans (Abel and MacKenzie, 1964), suggesting the possibility of increased light capture that may compensate the canopy size reduction. The ion toxicity and osmotic effects from salt stress may also have an impact on RUE, but no literature values can be found. The RUE and $\sum$APAR analysis should provide an useful framework for understanding salinity effects on plant growth.

The overall goal of the study was to characterize the relative importance of salinity effects on soybean $\sum$APAR and RUE at a whole plant level. More specifically, the study was conducted (1) to quantify canopy development, leaf chlorophyll, and (2) to determine $\sum$APAR and RUE for soybeans grown under either saline or non-saline conditions. For comparison, field and greenhouse experiments were conducted using similar salinity treatments and measurement procedures.

2. Materials and methods

2.1. Theoretical analysis

For plants growing with sufficient water and nutrients, biomass dry matter (DM) production is proportional to the cumulative PAR (400–700 nm) absorbed by the plant canopy (Green, 1987). The relationship between DM and RUE and PAR can be described with a simple integral function first proposed by Monteith (1977):

$$\mathrm{DM} = e_\mathrm{i} \int_{t_0}^{t_1} \alpha f_\mathrm{I} (\beta R_\mathrm{s})\, \mathrm{d}t \tag{1}$$

where DM is in g m^{-2} and is e_i the RUE in g MJ^{-1}. The subscript i denotes experimental or salinity treatments. Inside the integrand, parameters α and β are canopy absorptivity for PAR and the ratio of PAR to global solar radiation (R_s, in W m^{-2}), respectively. Parameter f_I describes the fraction of radiation intercepted by the plant canopy. All three parameters are dimensionless. Variable t, including the integration limits (t_0 and t_1), represents time in second during the growing season.

Among α, β, and f_I, parameter f_I is the most dynamic and changes with time, location, plant species, and the stage of growth. This parameter is easily estimated using Beer's law:

$$f_\mathrm{I} = 1 - \mathrm{e}^{-K\mathrm{LAI}} \tag{2}$$

where K is the canopy extinction coefficient, indicative of canopy characteristics and light source, and LAI is the leaf area index. The extinction coefficient

for direct solar beam radiation (K_{be}) can be calculated from (Campbell and Norman, 1998):

$$K_{be} = \frac{\sqrt{x^2 + \tan^2\psi}}{x + 1.774(x + 1.182)^{-0.733}} \quad (3)$$

where x represents leaf angle distribution, a function of canopy structure (≈0.81 for soybeans under no salinity stress, Campbell and van Evert, 1994) and ψ is the solar zenith angle, which can be computed from the latitude, longitude, and the time of measurement.

2.2. Field experiment

A field experiment was conducted between June and October 1998 at the University of California Agriculture Experiment Station at Riverside, CA (33°58′23″N; 117°20′30″W; 258 m above sea level). The soil at the study site is an Arlington fine sandy loam (coarse-loamy, mixed, thermic, Haplic Durixeralf) with a particle size distribution consisting of 63% sand, 30% silt, and 7% clay.

To impose a salinity effect, the soil in the salinity treatment plot (12 m × 76 m) was salinized with a NaCl and $CaCl_2$ mixture (at 1:1 weight ratio and 1.8 Mg ha^{-1} rate) using a sprinkler system before planting. Seeds of soybean (*Glycine max* (L.) Merr. cv. Manokin) were planted on 11 June 1998 or day-of-year (DOY) 162 in the salinity and an adjacent control plot (12 m × 76 m), and both plots had a row spacing of 0.8 m. Sprinkler irrigation with non-saline canal water ($EC_w \approx 0.5$ dS m^{-1}) was used until 40 days after planting to help soybean emergence and seedling establishment. Soybean seed emergence was measured 20 days after planting, and the seedling density found was 15 and 24 seedlings per square meter for the salinity and control plot, respectively. On 41 days after planting, the sprinkler system was removed, and the salinity and control plots were subsequently furrow irrigated with non-saline canal water.

The actual salinity levels in the soil were measured from three replicated core samples taken at the center of both field bed and furrow locations on dates near the beginning (DOY 180) and end (DOY 321) of the experiment. Electrical conductivity of the sample solution paste extract (EC_e) was used to describe soil salinity levels. Because soil water content changed significantly with depth and location, the measured EC_e values were normalized to a constant water content value of 0.15 cm^3 cm^{-3}. This value corresponded to the water content at −10 kPa, which was near field capacity. A weather station was installed at the field site, and meteorological parameters such as incoming global solar radiation (R_s) were continuously recorded during the experiment.

To obtain plant biophysical parameters for the determination of $\sum$APAR and RUE, nine soybean plants were harvested from both the salinity and control plots on DOY 201, 222, 243 and 264, respectively. To minimize dehydration and tissue breakdown, the plants were stored in cooled ice chests immediately after harvest and transported to the laboratory where they were separated into leaf, stem, root and pod (when present). Total leaf area of each plant was measured by passing individual leaflets through a LICOR LI-3100 leaf area meter (LI-COR, Lincoln, NE).[1] LAI was calculated as the ratio of green leaf area divided by the total ground area each plant occupied. Leaf chlorophyll was determined from nine leaves found in the upper canopy of each plant using a SPAD-502 meter (Spectrum Technologies, Plainfield, IL).[2] Calibration between the SPAD reading and leaf chlorophyll was made from leaf extracts using a Beckman DU 7500 spectrophotometer (Beckman Instruments, Fullerton, CA).[3] Leaf samples for the calibration were collected from both the salinity and control plots. Total canopy chlorophyll was computed as the product of chlorophyll per unit leaf area and LAI. To determine RUE, total above ground (shoot) and below ground (root) plant materials from the four harvests plus an additional harvest on DOY 292 were dried at about 70°C in a forced-air oven to constant weights.

Based on the measured global solar radiation at the field site, absorbed PAR (or APAR) was obtained over the season using the integral part of Eq. (1). For plants with full green canopies, APAR can be reasonably approximated with the intercepted PAR (Daughtry et al., 1992), which indicates small changes in parameter α. In this study, it was assumed to be a constant value of 0.943 according to the regression data from

[1] Mention of products and company names does not constitute endorsement by the USDA.

[2] See Footnote 1.

[3] See Footnote 1.

Daughtry et al. (1992). The parameter β was also assumed to have a constant value of 0.45 based on the measurements by Meek et al. (1984) in the western USA. The fraction of radiation intercepted by the soybean canopy (f_I), however, can change significantly with LAI and K. Whereas LAI was interpolated from the direct measurements of destructive plant samplings, the extinction coefficient (K) was computed hourly using Eq. (3). In determining K, the leaf angle distribution (x) was assumed to be 0.81 for soybeans in both the salinity and control treatments. The solar zenith angle (ψ) was calculated hourly for the duration of the experiment for the field location. To validate the computed APAR with direct field measurements, intercepted PAR above and below the soybean canopy was measured on DOY 226 and 244 with the LI-191SA line quantum sensor (LI-COR, Lincoln, NE).[4] The measurements on each date were repeated at multiple locations across the salinity and control plots, representing different LAI values which were measured with a LAI-2000 plant canopy analyzer (LI-COR, Lincoln, NE).[5] The intercepted PAR was then multiplied with α (0.943) to produce the measured APAR.

2.3. Greenhouse experiment

A greenhouse experiment was conducted between February and June 1999, also at Riverside, CA to support the results of the field experiment. The separate greenhouse experiment provided a more precise control of substrate salinity than in the field experiment. Soybean seeds were planted on 9 February 1999 or DOY 40 in six sand tanks (120 cm long, 60 cm wide, and 40 cm deep) filled with No. 12 silica sand (diameter $\approx$ 1.2 mm). From the time of planting, the sand tanks were irrigated three times daily with a modified Hoagland's nutrient solution (solution composition from Maas and Grieve (1990)). Each irrigation cycle continued for 12 min until the sand was completely saturated. The solution was then drained into two 765 l reservoirs for reuse in the next irrigation cycle. Each reservoir was connected to three sand tanks forming a closed system. Three tanks that were connected to one of the reservoirs were randomly selected as the control treatment, and irrigated with the nutrient solution ($EC_w \approx 1.6\,dS\,m^{-1}$) for the duration of the experiment. The remaining three tanks connected to the other reservoir were used for the salinity treatment. Mixed salts (NaCl and $CaCl_2$ at 1:1 weight ratio) were added incrementally to the nutrient solution in the salinity reservoir over five consecutive days to give a final EC_w of 9.7 dS m^{-1} by DOY 58. This value was similar to the salinity levels in the field experiment and was maintained until the end of the experiment. The gradual increase of solution salinity was to prevent a sudden osmotic shock to the soybean seedlings.

Nine soybean plants were harvested biweekly from the salinity and control treatments for growth parameter measurements. Again, canopy LAI was calculated as the ratio of green leaf area divided by the ground area, and leaf chlorophyll was determined from the SPAD-502 meter readings with a new calibration curve. Similar to the field experiment, biomass DM production was obtained from oven-dried plant parts for RUE estimation.

A pyranometer and a quantum sensor were placed at plant height for measurements of R_s and PAR. Both sensors were raised weekly to a height about 5 cm above the canopy to reduce the effect of light obstruction, reflection, and attenuation from the greenhouse building structures. Nearly identical readings were obtained from both sensors, which indicated a filtering effect of light spectra outside PAR by the greenhouse roof glass. Therefore, a unit value was used for parameter β. Other parameters required for Eqs. (1)–(3) were the same as used in the field experiment.

3. Results and discussion

3.1. Prediction of K and APAR and measured soil salinity

Despite differences in locality, predicted soybean extinction coefficients from Eq. (3) compared reasonably well with literature values for different hours on day 200 (Fig. 1a) and at noon for different dates during a year (Fig. 1b). The computed hourly APAR was strongly correlated to measured values (Fig. 2), therefore, it was reasonable to use the predicted K, and

[4] See Footnote 1.
[5] See Footnote 1.

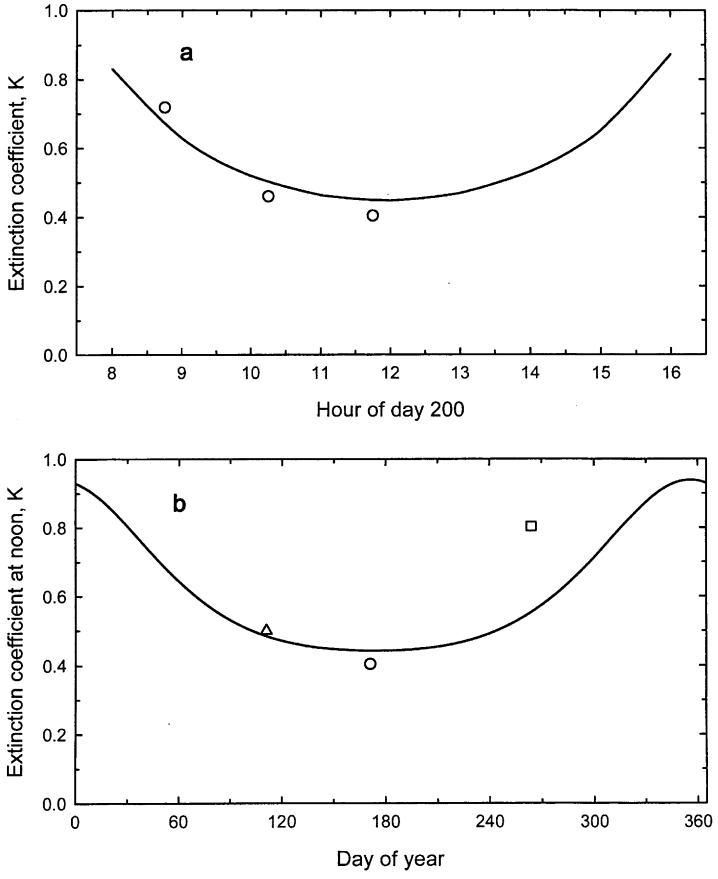

Fig. 1. Soybean extinction coefficients. Lines represent extinction coefficients for direct beam radiation predicted with Eq. (3) for Riverside, CA, USA (33°58′N, 117°20′W) for different hours on day 200 (a) and at noon for different dates during a year (b). Open circles are from Flénet et al. (1996). The open triangle is from Pengelly et al. (1999) and the open square is from Daughtry et al. (1992).

measured LAI and R_s as inputs to estimate the actual APAR. The strong correlation also provided a validation of holding the leaf angle distribution parameter as a constant value $(x = 0.81)$ for both salinity and control treatment.

Near the beginning of the field experiment (DOY 180), soil EC in the salinity plot was about 10 dS m^{-1} at 10–40 cm depth. Soil EC in the control plot was relatively uniformly distributed over depth and was generally less than 5 dS m^{-1}. Therefore, the preplanting salinization raised soil salinity in the salinity plot to levels significantly higher than those in the control. Over time, average soil EC in the salinity plot, except at the bed surface 15 cm, remained about 10 dS m^{-1} during the growing season. Average soil salinity in the control plot remained less than 5 dS m^{-1}, which is the threshold value for soybeans before significant yield reduction occurs (Maas and Hoffman, 1977).

3.2. Soybean LAI and leaf and canopy chlorophyll

In the field, the effect of salinity on LAI reduction started to occur on DOY 201 and continued to the end of season (Fig. 3a). This would very likely reduce APAR because of the reduced total leaf area. Leaf chlorophyll in the salinity plot, however, exceeded that in the control plot from about DOY 213 and remained higher until final harvest (Fig. 3b). Our visual observation also indicated that plants in the salinity plot had smaller and darker green leaves than those in the control plot. A simple explanation is that salinity reduced the rate of cell expansion that would result

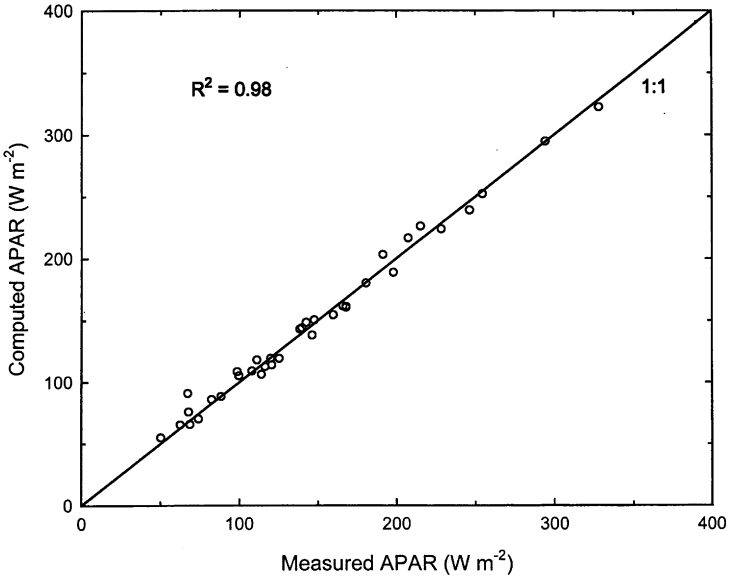

Fig. 2. Comparison of measured and computed PAR absorbed by soybean canopy (APAR).

in concentrating chloroplasts within plant cells (Nieman, 1965). Total canopy chlorophyll per ground area, however, was still higher in the control than in the salinity treatment (Fig. 3c) due to the much larger leaf area in the control plot. The total canopy chlorophyll per unit ground area is a useful measure for determining the rate and amount of radiation that may potentially be transformed to plant biochemical energy. It is generally found that the density of leaf chlorophyll determines the number of active structural units of photosystems responsible for photophosphorylation (Charles-Edwards et al., 1986). Higher total canopy chlorophyll such as in the control plot (Fig. 3c) would translate likely to more sites for carbohydrate assimilation and DM accumulation.

Frequent sampling in the greenhouse experiment indicated that rapid canopy development (or LAI increase) occurred in the control treatment between DOY 98 and 126 (Fig. 4a). In the salinity treatment, however, no significant change in LAI was observed and canopy expansion appeared to have ceased by DOY 112. Over the course of the greenhouse experiment, leaf chlorophyll in the control treatment gradually increased from a low value of 0.19 g m^{-2} at the beginning to a maximum of 0.46 g m^{-2} near the end of peak vegetative growth (Fig. 4b). In the salinity treatment, however, it remained relatively constant at about 0.32 g m^{-2}. The apparent temporal increase of canopy LAI and chlorophyll in the control but not in the salinity treatment (Fig. 4a and b) clearly showed that salinity had a significant detrimental effect on soybean vegetative growth that can be quantified with plant biophysical and biochemical parameters. More importantly, a direct consequence of the deleterious effect was to reduce total canopy chlorophyll (Fig. 4c), especially during the very important podding and seed filling stages of plant growth (after DOY 100). Total canopy chlorophyll between DOY 126 and 153 averaged 0.73 g m^{-2} in the salinity treatment, which was only about half of that in the control (1.58 g m^{-2}).

3.3. Radiation absorption and RUE

Reduced soybean canopy development from salinity stress resulted in less radiation absorption than plants in the control plot. Soybeans in the control plot of the field experiment accumulated 583 MJ m^{-2} APAR at 110 days after planting, whereas plants in the salinity plot absorbed 457 MJ m^{-2} (Table 1), about a 20% reduction in $\sum$ APAR. Plants in the greenhouse experiment also received less PAR when irrigated with the salinized water. The salinity-induced reductions in $\sum$ APAR were directly related to decreases in LAI (Figs. 3a and 4a). On the average, $\sum$ APAR was larger

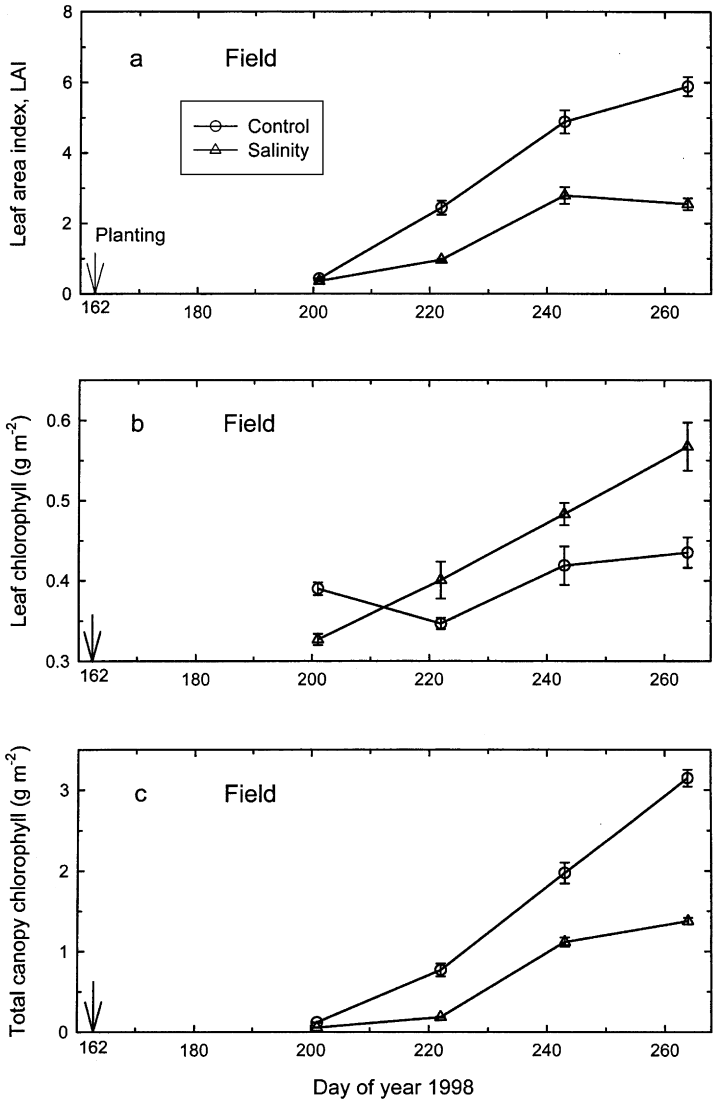

Fig. 3. LAI (a), chlorophyll (b), and total canopy chlorophyll (c) of soybean plants from 1998 field experiment. Bars represent ±S.E. ($n = 9$).

Table 1
Cumulative absorbed photosynthetically active radiation ($\sum$ APAR) at 110 days after planting and RUE for above-ground (RUE_{ag}) and total (shoot + root, RUE_{tot}) biomass DM for soybean (cv. Manokin) grown under either a saline or non-saline (control) environment[a]

Experiment	Treatment	$\sum$ APAR (MJ m^{-2})	RUE_{ag} (g MJ^{-1})	RUE_{tot} (g MJ^{-1})
Field 1998	Salinity	457	1.08b	1.15b
	Control	583	1.89a	2.14a
Greenhouse 1999	Salinity	711	0.61d	0.67c
	Control	758	0.95c	1.00b

[a] Values followed by different letters are significantly different at $P < 0.01$.

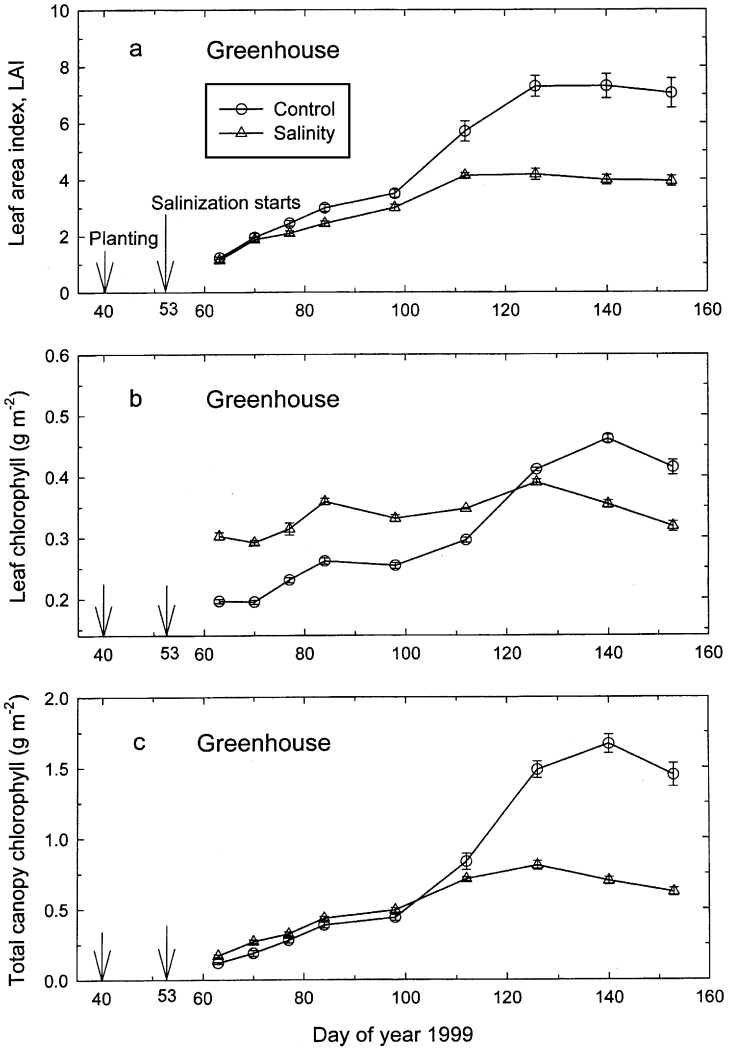

Fig. 4. LAI (a), chlorophyll (b), and total canopy chlorophyll (c) of soybean plants from 1999 greenhouse experiment. Bars represent ±S.E. ($n = 9$).

in the greenhouse than in the field experiment. This was expected because the greenhouse experiment was conducted in early spring when solar zenith angles (ψ) were large. For example, $\psi = 44.0°$ on DOY 54 during the greenhouse experiment; and $\psi = 10.7°$ on DOY 174 during the 1998 field experiment. The larger zenith angles would result in higher canopy extinction coefficients or more PAR interception.

Strong correlation was found between $\sum$APAR and above-ground and total plant biomass in both the salinity and control treatments for the field and greenhouse experiments (Fig. 5). Both above-ground and total plant biomass were analyzed because salinity was reported to affect plant shoot to root ratios (Maas and Hoffman, 1977). Regression analysis using Eq. (1) generated a RUE value (the slope) for each salinity and experiment combination (Table 1). The theoretical and experimental procedures used in this study were reasonable because the estimated RUE for above-ground biomass (RUE_{ag}) in the control plot of 1998 field experiment was 1.89 g MJ^{-1} $\sum$APAR, which was comparable to RUE_{ag} values reported in the

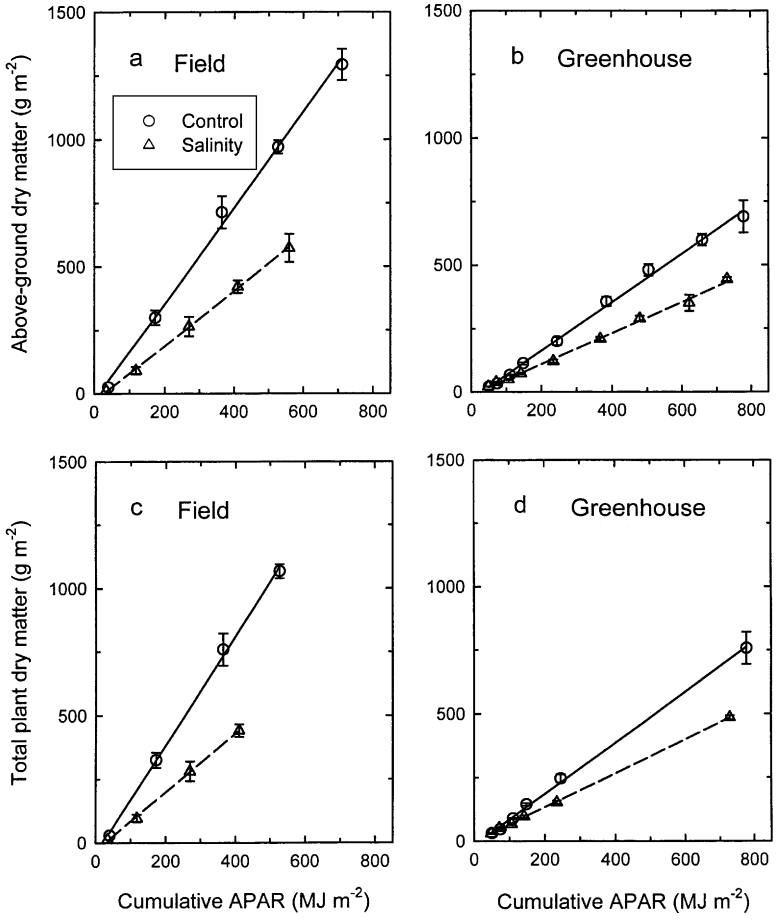

Fig. 5. Above-ground DM for the 1998 field (a) and 1999 greenhouse (b) and total plant DM (shoot + root) for the field (c) and greenhouse (d) soybean — salinity experiments shown as a function of cumulative absorbed photosynthetically active radiation (APAR). Bars represent ±S.E. ($n = 9$).

literature. Using a constant β value of 0.45, we converted soybean RUE_{ag} values found in the literature with respect to global solar radiation (R_s) to $\sum$APAR. The converted soybean RUE_{ag} values were 1.67 (Rochette et al., 1995), 1.93 (Board et al., 1994 for 50 cm row spacing), 1.96 (Muchow et al., 1993), 1.98 (Pengelly et al., 1999), and 1.59–2.34 g MJ^{-1} $\sum$APAR (Daughtry et al., 1992). Variations in the literature RUE_{ag} values were likely attributed to geographical and soybean varietal differences.

Comparison tests of regression lines, following procedures of Snedecor and Cochran (1967), showed that the imposed salinity stress significantly ($P < 0.01$) reduced RUE_{ag} and RUE_{tot} (for total plant biomass) in both the field and greenhouse experiments (Table 1). In both the field and greenhouse experiments, salinity stress was maintained throughout the vegetative and reproductive stages of growth. It was most likely that the consistent reductions in RUE were caused by significant osmotic and Na^+ and Cl^- toxicity stresses that translated to reductions in total canopy chlorophyll (Figs. 3c and 4c).

To further evaluate the effect of salinity on $\sum$APAR and RUE, data from a concurrent experiment conducted at the same field site to study the effect of salinity on emergence (Wang and Shannon, 1999), were analyzed to derive a set of $\sum$APAR and RUE_{ag} values for different soybean cultivars and

Table 2
Cumulative absorbed photosynthetically active radiation ($\sum$APAR) at 110 days after planting and RUE for above-ground (RUE_{ag}) biomass DM for soybean (cv. Lee and Essex) grown under either a saline or non-saline (control) environment[a]

Soybean cultivar	Maturity group	Treatment	$\sum$APAR (MJ m^{-2})	RUE_{ag} (g MJ^{-1})
Lee	IV	Salinity	454	0.83a
	IV	Control	595	1.12a
	V	Salinity	388	1.14a
	V	Control	616	1.79b
	VI	Salinity	460	1.25a
	VI	Control	592	2.24c
	VII	Salinity	473	1.20a
	VII	Control	560	2.27c
Essex	V	Salinity	485	1.13a
	V	Control	619	1.49b
	VI	Salinity	416	1.18a
	VI	Control	613	1.31a
	VII	Salinity	477	1.18a
	VII	Control	580	1.48b

[a] Values followed by different letters are significantly different at $P < 0.01$.

maturity groups (Table 2). Similar to the main field experiment on cultivar Manokin, salinity reduced $\sum$APAR for both the Lee and Essex soybeans. The $\sum$APAR values were calculated from the measured LAI following the same procedures as for the main experiment. Except for Lee-IV and Essex-VI, RUE_{ag} was significantly reduced by the salinity stress. It was impossible to estimate RUE_{tot} for the Lee and Essex soybeans because no root samples were taken.

In summary, results from the study indicated that a substrate salinity of about 10 dS m^{-1} significantly reduced soybean canopy size (or LAI), but increased leaf chlorophyll content for much of the growing season. The reduction in LAI was attributed to smaller plant and leaf sizes, whereas the increase in leaf chlorophyll was related to the observed darker green leaves when stressed by salinity. The degree of LAI reduction exceeded small gains in leaf chlorophyll because the total canopy chlorophyll per unit ground area was smaller when under salinity stress. Reasonable estimates were obtained for APAR by soybean canopies based on hourly inputs of predicted K, interpolated LAI, and R_s values measured above the plant canopy. A continuous salinity stress with a substrate EC of about 10 dS m^{-1} reduced both $\sum$APAR and RUE of the three soybean cultivars (Manokin, Lee, and Essex). Whereas it is conceivable that reductions in LAI resulted in less $\sum$APAR, salinity-induced reductions in RUE were attributed to the reductions in total canopy chlorophyll on a whole plant scale and to other potential mechanisms that would reduce the efficiency of biomass assimilation per unit APAR. If functional relationships can be established between the rate of biomass production and total canopy chlorophyll per unit PAR and LAI values and considering a reduction factor for salinity stress, a predictive model is possible for estimating salinity effect on biomass production. The advantage of the biophysical modeling approach over traditional plant salt tolerance assessments is that plant APAR and total canopy chlorophyll can be estimated remotely over large areas using remote sensing techniques (Gitelson and Merzlyak, 1996; Moran et al., 1995).

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